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# **THE NEURAL BASIS AND FUNCTIONAL CHARACTERISTICS OF PERIPHERAL VISION**

**AFOSR Grant No. F49620-95-1-0509**

## **FINAL TECHNICAL REPORT**

### **Introduction and Background**

This Report describes a program of work undertaken in the final extension of a sequence of AFOSR awards:

- Grant No F49620-95-1-0509: This one-year award of \$50,050, made in January 1995, was used principally to cover the salary of a postdoctoral researcher, Dr Jack Scannell.
- Special Contract Program No SPC-95-4046, totaling \$100,000, which commenced in September 1995, was used to fund the continuation of a postdoctoral salary at Oxford and also collaborations with the University of California, Davis, the Faculty of Medicine of Charles University, Hradec Kralové, Czech Republic and the University of Amsterdam, the Netherlands.
- Grant No F49620-95-1-0509 (extension): This continued funding (\$50,050, \$63,753 and \$135,732), extended from August 1996-August 1998, for the completion of the project.

The majority of the work was done at the University of Oxford, but the program included collaborations with:

- 1) Drs Fred Previc and Jeremy Beer of Brooks AFB and Drs Peter Fox and Mario Liotti of the Research Imaging Center, University of Texas, San Antonio.
- 2) Dr Ron Mangun of the University of California, Davis, California.
- 3) Drs Miroslav Kuba and Zuzana Kubova of the Faculty of Medicine of Charles University, Hradec Kralové, Czech Republic.
- 4) Professor Henk Spekrijse at the University of Amsterdam, the Netherlands

### **Abstract**

This project studied the processing of visual information, especially in the periphery of the visual field, employing several techniques (single-unit recording and optical recording from the cortex in anesthetized and unanesthetized animals; psychophysics, dense-array recording of event-related potentials and functional neuroimaging (PET and fMRI) in human volunteers and patients with brain damage). Peripheral vision is important not only because it selects and directs fixation towards interesting visual targets for detailed processing by foveal visual mechanisms, but also because it plays a vital role in visuomotor coordination, posture and locomotion through space. These studies provided information about the role of the peripheral field in visual perception, especially the detection of optic flow, and the neural limitations on the detection and analysis of motion, in such skills as flying.

#### **SUBJECT TERMS:**

OPTIC FLOW; MOTION PERCEPTION; VESTIBULAR SYSTEM; VISUAL CORTEX; SINGLE NEURONS; NAVIGATION; MIDDLE TEMPORAL AREA; 'BLINDSIGHT'; BRAIN DAMAGE

## **Theoretical studies**

### **New Approaches to the analysis of brain connectivity**

Structures in the central nervous system typically make many connections with other structures. The primary visual cortex, V1, for example, exchanges substantial numbers of projection fibers with at least 60 other cortical and subcortical regions. This profuse connectivity is shared by most other structures in the central nervous system, so that the brain, at one level, can be thought of as a complex wiring network. Considering only the cerebral cortical part of this network, there are approximately 1000 reported ipsilateral corticocortical connections areas in the cat and monkey (Scannell and Young 1993; Young 1993; Scannell et al. 1995; Young et al. 1995). The complexity of even this part of the central nervous network is too great to allow conclusions about its organization to be drawn by unaided intuition. It has become an article of faith for many researchers, however, that connectivity data hold an important key to unraveling principles of brain organization (e.g. Rockland and Pandya 1979; Felleman and Van Essen 1991; Livingstone and Hubel 1988; Young 1992).

The complexity of the data, and the promise that they hold for providing insight into the organization of central nervous processing, have encouraged the development and application of data analytic methods for treating connection data systematically. Several methods have recently been applied to the problem of untangling the central nervous system's connectivity, including hierarchical analysis (Rockland and Pandya 1979; Maunsell and Van Essen 1986; Felleman and Van Essen 1991), cluster analysis (Musil and Olson 1991), hodological analysis (Nicollelis et al. 1990), and nonmetric multidimensional scaling (NMDS; Shepard 1980) (Scannell and Young 1993; Young 1992; 1993).

The group in Oxford led the development and use of the NMDS approach, and we have applied it widely. Every major sensory system in the cat and monkey cortex, and the gross cortical organization of each animal, were analyzed in this way (Scannell and Young 1993; Young 1992; 1993; Young et al., 1994a, 1994b; Scannell et al. 1995; Young et al., 1995). In this approach, connection data are considered to indicate the proximities between brain structures in a high-dimensional "connection space", and NMDS is used to reduce the number of dimensions of the space to make the configuration defined by the connections more understandable. The results of these analyses indicate that all the major cortical sensory systems in cats and monkeys are hierarchical, serially-ordered structures. In addition, the NMDS analyses of all the available cortical connection data suggest that both the monkey and cat cortical networks are divided into three major hierarchically-organized sensory systems, and a fourth system composed of prefrontal and limbic structures, which is connectionally distant from the sensory-motor periphery (Scannell and Young 1993; Young 1992; 1993; Young et al. 1995; Scannell et al. 1995).

If the widely held assumptions about the importance of connectivity are true, and if the methods that we have applied to its analysis are appropriate, we should be able to use them to guide empirical experiments in brain function. In fact, our new approaches to the analysis of cortical connectivity successfully drove a series of experiments on a higher-order motion processing area in the cat.

## **Studies of single neurons**

### **Motion processing in the cat cortex**

Any animal that moves around in the world needs to identify the directions of motion of objects and

surfaces, especially in the peripheral field, where image slip produced by self-motion is greatest, and where the direction of such slip provides valuable information about the trajectory of self-movement. Knowledge of motion can be used not only for navigation, but also to tie the direction of gaze to the environment, and to track objects of interest. Motion cues can also define contours, group objects, and signal 3-dimensional shape. Neurons that signal direction of motion seem to be ubiquitous in animals with well developed visual systems and, among the vertebrates, have been found in the retinae of frogs, pigeons, rabbits, ground squirrels, and cats and in the visual cortex of cats and monkeys (Hildreth and Koch 1987). However, in the striate cortex of the cat and monkey, and the extrastriate area PMLS of the cat, such cells are generally 'component motion (CM) selective', signaling only the direction of movement orthogonal to the preferred orientation; a direction that is not necessarily the same as the motion of the entire pattern or texture of which the cell's preferred contour is part (Movshon et al. 1985; Gizzi et al. 1990). The primate extrastriate middle temporal area (MT or V5) is the only cortical region currently known to contain a substantial population of 'pattern motion (PM) selective' cells, which respond to the shared vector of motion of mixtures of contours, such as two superimposed drifting gratings of different orientation - a 'plaid' (Movshon et al. 1985; Rodman and Albright 1989; Stoner and Albright 1992).

If connectivity is important in defining the function of the cortical network, then there should be a clear relation between the connections of cortical areas and what the areas do. However, there are now so many known connections between so many cortical areas that casual inspection of the primary connection data is no longer appropriate (Young 1992; Scannell and Young 1993; Scannell et al. 1995).

In the hope of identifying a cortical area in the cat likely to be involved in the high-level analysis of motion in the peripheral field, we examined representations of cortical connectivity derived from NMDS analysis (see Scannell et al. 1995 for more details), looking for an area towards the top of the visual hierarchy and closely connected with motor structures, especially the frontal eye fields. The candidate area that we identified was the tiny visual area in the anterior ectosylvian sulcus (AES); which we have called AEV (the anterior ectosylvian visual area). This area is unusual in that it is far anterior to the classical visual areas of the occipital cortex, and is adjacent to auditory fields. Indeed, it is surrounded by a region of multimodal cortex in which neurons respond to visual and auditory stimuli.

We conducted a thorough, quantitative analysis of the properties of individual neurons in AEV, using computer-generated visual stimuli (including moving gratings and plaids). Our results can be summarized as follows (see Scannell et al. 1994; 1995b; 1996):

- 1) AEV is indeed a higher-order motion area. 90% of AEV cells that responded strongly to drifting grating and/or plaid (mixed grating) stimuli were directionally selective (directionality index (DI) > 0.5). For this group, mean DI = 0.75. Moreover, 55% of these cells were unequivocally classified as pattern motion (PM) selective and only one neuron was classified as definitely component motion selective. Surprisingly, then, the proportion of PM selective neurons in this area is enormously higher than in the classical motion area MT of the macaque. Thus, high-level pattern-motion coding occurs in the cat extrastriate cortex and is not limited to primate area MT.

- 2) AEV contains a heterogeneous population of direction-selective cells. There was no clear relation between the degree of directional selectivity for plaids or gratings and the degree of selectivity for pattern motion or component motion. Nevertheless, the 28% of the highly responsive cells were both more strongly modulated by plaids than gratings and more PM selective than CM selective. Such cells

could correspond to a population of 'selection units' (Nowlan and Sejnowski 1995) - a specific class of motion selective 'units' that a recent model suggests signal the salience of local motion information, overcoming some of the problems of transparency of contradictory local motion cues.

3) AEV lacks global retinotopic order: the receptive fields of neurons recording in oblique penetrations wander in an apparently random way across the visual field, with no systematic topological relationship between the coordinates of the visual world and those of the cortical surface.

4) On the other hand, there is a striking mapping of the preferred direction of motion of neurons across this small region of cortex. Now, in monkey MT and cat PMLS, cells are clearly arranged in functional 'columns' such that all neurons encountered in penetrations orthogonal to the cortical surface have very similar preferred orientation. In the rhesus monkey (Albright et al. 1984), these columns seem to consist of pairs of adjacent hemi-columns having the same preferred contour orientation and the same preferred **axis** of motion but opposite preferred directions in the two hemi-columns. The preferred **axis** of motion shifts progressively from one column pair to the next across MT. Thus the features that are mapped across MT are axis-of-motion and contour orientation, rather than direction of motion *per se*. Each complete cycle of representation or "hypercolumn" (Hubel and Wiesel, 1974) across the cortex covers  $180^\circ$  of orientation or motion axis, rather than a continuous cycle of  $360^\circ$  of direction. This form of mapping, with adjacent columns for opposite directions, results in frequent  $180^\circ$  shifts of preferred direction from one cluster of cells to the next during oblique penetrations, as the electrode crosses the boundary between an opposed motion hemi-column pair (Albright et al. 1984). However, in AEV, the preferred direction (rather than the preferred axis or orientation) is mapped systematically across the cortex. From column to column there are small, progressive shifts in preferred direction, with none of the  $180^\circ$  changes seen during long penetrations through PMLS and MT. This strongly suggests that AEV is a non-retinotopic, feature-mapped area in which cells representing similar parts of 'motion space' are brought together on the cortical sheet (Barlow 1981). It consists of smooth sequences of individual direction domains with the full cycle of  $360^\circ$  (a directional hypercolumn) extending over some 1.5 to 2.0 mm of the cortical surface in the coronal plane. Since the entire visual area is only about 4 mm in diameter or less, AEV must contain a very small number of directional hypercolumns - conceivably only one or two.

In these respects - direction mapping and PM selectivity - AEV seems even more committed to the analysis of directional motion than is MT. Moreover, unlike MT, it has no global retinotopic order. The fact that AEV brings together information about the same direction of motion from different regions of visual space suggests that it might be involved in the segregation of moving objects and surfaces on the basis of shared direction of motion, a process that is performed over extensive regions of visual space in human perception. These results have been published in full (Scannell et al. 1996).

In his Ferrier Lecture, Horace Barlow (1981) predicted the existence of non-topographic, feature-mapped cortical areas to perform segregation tasks involving the detection of coincident stimulus characteristics across wide regions of the field. AEV may be such an area. This feature of the organization of AEV has lead on to a series of experiments to investigate the local mapping of motion in more detail and these are considered in the next section.

### **The neural basis of binocular rivalry and suppression**

Head-mounted displays for cockpit use face an unavoidable trade-off between resolution and field size. In an attempt to mitigate this problem, one strategy, being developed by Dr Brian Tsou and his

colleagues at the Armstrong Laboratory, Wright-Patterson AFB, Ohio, is to use binocular displays that are only partially superimposed, in the centre of the field, thus increasing the overall width of the display (Grisby and Tsou, 1994). However, a potential problem with this approach is that the more peripheral parts of the display, on each side, well within the region of normal binocular overlap of the two eyes, are viewed by only one eye. Hence dissimilar images (the display and the view of the external world) fall on the peripheral field of the two eyes. In central vision, the viewing of dissimilar images produces a powerful and disturbing perceptual phenomenon called *binocular rivalry*. The two images are not seen fused: instead the pattern breaks up into fluid patches, within which each eye's image is alternately suppressed and the other one dominates, every few seconds.

The mechanism of normal binocular vision is thought to involve cortical neurons that unite the information generated by each eye in a common stream that eventually leads to perception. The small positional differences in the retinal images of the two eyes associated with viewing objects at different distances cause selective stimulation of neurons 'tuned' to different retinal disparities (Barlow, Blakemore and Pettigrew, 1967), and hence stereopsis. If the disparities are not large, perceptual fusion still predominates. If, however, the right and left eyes are stimulated with highly discrepant visual scenes, binocular rivalry ensues, in which the two images compete for perceptual dominance (Wheatstone, 1838). Binocular rivalry has traditionally been explained in terms of suppression of one or other input at the level of monocular representation (cf Asher, 1953), i.e. at the lateral geniculate nucleus or layer 4 of the primary visual cortex.

### Rivalry

A major interest of the research group in Oxford, supported in part by the AFOSR grant, has been in the neural basis of binocular rivalry, and of the related condition of *strabismic suppression*, experienced by individuals with strabismus, in which the fixating eye continuously 'suppresses' the image in the non-fixating eye. Traditionally, both forms of interocular suppression have been attributed to inhibition operating at a very peripheral level in the visual system, where the signals from the two eyes are still completely segregated, i.e. the lateral geniculate nucleus (LGN) or layer 4 of the primary visual cortex (Blake, 1989; Lehky and Blake, 1991).

In an attempt to demonstrate a physiological basis for rivalry, we studied the responses of neurons in the LGN and area 17 of cats, and monkeys, for drifting gratings of different orientation, spatial frequency and contrast in the two eyes (Sengpiel and Blakemore, 1994; Sengpiel et al. 1995a, 1995b, 1995c).

Almost half the LGN neurons studied exhibited modest inhibitory interocular interaction, but independent of interocular differences in orientation, and therefore inappropriate to explain the highly orientation-dependent nature of binocular pattern rivalry. Monocularly driven units in layer 4 of area 17 behaved similarly. However, for the majority of binocular cortical cells, the response to a grating of optimal orientation in one eye was suppressed by a grating of sufficiently different orientation shown to the other eye, over a wide range of spatial frequency and independent of relative spatial phase. This interocular suppression exhibits a remarkable non-linearity: a grating of non-preferred orientation in one eye causes significant interocular suppression only if the neuron is already responding to an appropriate stimulus in the other eye (Sengpiel and Blakemore, 1994).

We propose that the switches in perceptual dominance during binocular contour rivalry depend on interocular interactions at the level of binocular neurons of the primary visual cortex, which might involve intracortical inhibition between adjacent ocular dominance columns. The spontaneous alternations in perceptual suppression that occur during prolonged viewing of rivalrous patterns remain

to be explained, although significant variation in the strength of neuronal suppression in such conditions was occasionally seen.

### **Strabismic suppression**

Strabismic humans usually experience powerful suppression of vision in the non-fixating eye. In an attempt to demonstrate physiological correlates of such suppression, we recorded from the primary visual cortex of cats with surgically-induced squint and studied the responses of neurons to drifting gratings of different orientation, spatial frequency and contrast in the two eyes. (Sengpiel et al. 1994). Only 1 out of 50 apparently monocular cells showed any evidence of remaining, subliminal excitatory input from the 'silent' eye when the two eyes were stimulated with gratings of similar orientation and even among the small proportion of cells that remained binocularly driven, very few exhibited facilitation when stimulated binocularly. The majority of cells from both exotropes and esotropes, even those that could be independently driven through either eye, displayed non-specific interocular *suppression*: stimulation of the non-dominant eye with a drifting grating of *any* orientation depressed the response to an optimal grating being presented to the dominant eye. This phenomenon exhibited a gross non-linearity in that it was dependent on the temporal sequence of stimulus presentation: stimulation of the non-dominant eye caused significant suppression only if the neuron was already responding to an appropriate stimulus in the dominant eye, but not when onset of stimulation in the two eyes was simultaneous. Interocular suppression was always independent of the relative spatial phase of the two grating stimuli, and usually broadly tuned for the spatial frequency of the suppressive stimulus. Suppression may depend on inhibitory interaction between neighboring ocular dominance columns, combined with the loss of conventional disparity-selective binocular interactions for matched stimuli in the two eyes. The similarity of interocular suppression in strabismic cats and that caused by orthogonal gratings in the two eyes in normal cats (Sengpiel and Blakemore, 1994; Sengpiel et al., 1994) suggests that strabismic suppression and binocular rivalry depend on similar neural mechanisms.

### **Pattern-motion selectivity in the monkey primary visual cortex: evidence for the function of back-projections from extrastriate to primary visual cortex**

#### **Background**

In the primate brain, motion information is processed in an hierarchical manner. Psychophysical evidence suggests that motion processing in humans also happens in at least two stages (Stoner and Albright, 1994). In the first stage, orientation- and spatial frequency-selective mechanisms compute motion signals within local regions of visual space. Such signals are combined according to simple geometric rules at the second stage of motion processing, where the direction and velocity of complex moving objects are represented (Movshon *et al.*, 1985; Ferrera and Wilson, 1990; Wilson *et al.*, 1992). Physiological recording from the visual cortex of **anesthetized** monkeys has revealed potential correlates of these two stages in striate cortex (V1) and the extrastriate middle temporal area (MT or V5) respectively (see Movshon *et al.* 1985; Logothetis, 1994). In V1, as described above, direction-selective neurons are generally component-motion (CM) selective: they respond to the direction of movement orthogonal to the preferred orientation, a direction that is not necessarily the same as the motion of the entire object or surface of which the cell's preferred contour is part. In contrast, a population of neurons in MT (or V5) are pattern-motion (PM) selective, integrating components of motion vectors from various edges in an object into a more global representation of the true direction of object motion. Thus, MT appears, from studies in anesthetized monkeys, to provide the second stage of analysis of signals from V1 (Movshon *et al.*, 1985; Ferrera and Maunsell, 1991; Rodman and Albright, 1989; Orban, 1994; Movshon and Newsome, 1996; Andersen, 1997).

CM and PM selectivities are conventionally distinguished by comparing the responses of a particular neuron to a single drifting grating, presented at several different directions of drift, with those to a 'plaid' pattern, consisting of two superimposed drifting gratings, locked together with a certain angle between the two component gratings. Such a plaid is normally perceived by human (and monkey) observers as moving in a single direction, corresponding to the shared vector of motion of the two component gratings (the bisector of the two directions if their velocities are identical). However CM selective neurons simply respond independently to each of the components of such a drifting plaid, thus responding maximally to two different directions of the plaid drift (separated by an angle equal to the angle between the two orientations of the plaid), at which each of the component gratings appears at the optimum orientation/direction in the cell's receptive field. PM selective neurons respond best when the plaid is moved in the same direction as the optimal direction for a single grating. Thus, a true PM cell behaves in a manner appropriate to signal the direction of motion actually perceived.

Back-projections, i.e. pathways passing back to 'lower' cortical areas from areas presumed to be higher in the assumed serial hierarchy, are a ubiquitous feature of the array of visual cortical areas. The density of such back-projections (sometimes involving as many axons as in the forward pathway) suggests that they plan an important function, yet there is no clearly established view of what that function might be. We are considering the hypothesis that they inform lower visual areas of the results of processing in higher areas, especially when those higher computations involve analysis of a wider range of features or a larger area of the visual field than is available directly within the classical receptive fields of neurons in lower areas.

Over 90% of the back-projections from MT target V1 and terminate in layer 4B - the layer that contains the population of CMS cells that provide the forward-projecting input to MT. We propose, then, that the computed property of pattern-motion selectivity might be fed back to cells of V1 under conditions in which a monkey (or a human) is perceiving the true direction of motion of surfaces and objects.

We have recorded extracellularly from neurons in V1 in trained animals to see whether neurons in layers 4B (and layer 6, where direction-selective cells are also found) also exhibit pattern-motion selectivity in the alert animal. As a control, we have also recorded from the primary visual cortex of anesthetized macaque monkeys, to replicate previous results.

## Methods

During the period of support from the US Air Force, we established a laboratory for recording in awake, trained monkeys. Computer software was written to train the animals, record single unit activity and monitor eye movements, using the magnetic coil technique. In each of two adult macaques (*Macaca mulatta*), a scleral search coil, single-unit recording chamber and head fixation device were implanted under aseptic conditions. The activity of single units in V1 was recorded with tungsten microelectrodes. These two monkeys were trained to fixate a small fixation point ( $0.2^\circ$  diameter) for several seconds, without looking at any other visual stimulus simultaneously present on the display (see Guo and Li, 1997). After receptive field (RF) characteristics had been determined, drifting sinusoidal gratings (of optimal spatial and temporal frequency of drift) and plaids were presented to the RF. These stimuli were presented at 16 orientations/directions ( $22.5^\circ$  increments) in a random order, repeated 5 times. The two components in the plaid patterns were usually separated by  $90^\circ$ ; but we also tested some units with  $135^\circ$  component-separated plaids.

## Results



Out of a total of 212 neurons recorded in and around layer IV of the primary visual cortex (judged by electrode depth), 60 cells were both strongly driven by drifting gratings and were highly direction selective (direction index  $> 0.5$ ). Fifty five of these directional cells were thoroughly tested with drifting plaids as well as moving gratings.

We used a partial correlation coefficient, adapted from Movshon *et al.* (1985), to classify the direction-selectivity of cells quantitatively. Fully 9% of the 55 directional cells tested were unequivocally **pattern-motion** selective. For these cells, the tuning curves for drifting plaids had a single lobe, peaking at the shared vector of the two components and similar in width to the tuning curve for a single grating, just as for the best examples from MT in the anesthetized monkey. 30 neurons were clearly component-motion selective, but the remaining 20 cells lay within the 'unclassified' portion of response space, biased, if anything, towards PM selectivity.

In control experiments, we used identical techniques for stimulus generation and data analysis to study responses from single neurons recorded in **anesthetized** macaques (and also, for comparison, cats). Not a single neuron, out of all those that were classified as strongly direction-selective on the basis of responses to plain gratings, showed a clear tendency towards PM selectivity. Indeed, 72% were unequivocally CM selective, and those that lay in the unclassified section of the correlation space were strongly biased towards CM selectivity.

Thus, we were able to reproduce previous results, showing that the primary visual cortex in anesthetized animals, is incapable of performing the integration of local motion that is required for PM selectivity. However, the characteristics of direction-selective cells in layer IV of the primary cortex of the awake monkey closely resemble those of cells in MT. Now, the directional cells of layer IV provide the input to MT (which is presumed to be integrated there to generate PM selectivity). But layer IV is the main target of the dense feedback projection from MT to V1. Our results strongly imply that the back-projection from MT imposes PM selectivity on the very neurons that provide the input to MT.

This back-projection could, then, be viewed as providing V1 with the results of neural computations performed in MT, of which V1 itself is incapable. This may be a general feature of feedback from non-primary to primary sensory areas. The array of non-primary fields that surround primary sensory areas in higher mammals may have evolved to carry our computations requiring properties (such as access to information from a wide area of visual field), which do not exist in the primary area.

## Optical imaging of intrinsic signals in visual cortex

### Background

During the period of the AFOSR grant we acquired (through funding from the UK Medical Research council) a facility for imaging activity in the exposed cortex of anesthetized animals by optical recording of intrinsic signals related to the deoxygenation of hemoglobin and changes in local blood flow. We have used this technique, partly with support from the AFOSR grant, to investigate the organization of primary visual areas in cats and marmosets. Three investigations have been pursued.

#### 1. *Primary and secondary visual areas*

The aim of this work was to increase our understanding of the processing in these brain regions, which are crucial for vision and which have analogs in the primate brain. Various stimulus manipulations are used to try to understand the different kinds of processing carried out in each area. So far we have concentrated on the different sensitivities of cells in V1 and V2 to the spatial

frequency and contrast of moving grating patterns.

2. *Depth processing in the visual cortex*

We have investigated whether neurons that respond selectively to different retinal disparities are organized together into local processing modules in the primary and secondary visual cortices of the cat - a finding that would support the hypothesis that these peripheral visual areas are involved in representing three-dimensional visual space.

3. *Visual function in the marmoset*

The marmoset is a New-world monkey ideally suited to investigation using optical imaging. It has well developed visual abilities, on a par with humans, but, unlike in Old-world primates, the cortical sheet is both small and smooth, unperturbed by sulci and gyri. This means that all brain areas are available for investigation by optical imaging and that several different extrastriate areas can be simultaneously imaged.

### Methods

Optical imaging (Grinvald *et al.*, 1986) allows the simultaneous recording of activity in large areas of the cerebral cortex. The underlying principle is that areas of brain that are more active during a given task will have an increased blood supply (the same principle underlies PET and fMRI imaging techniques). In optical imaging the increased neural activity in an area can be detected by shining light of a certain wavelength on to the cortex and observing the changes in absorption due to the changes in blood supply in a particular area. The optical signal measured by a video camera is a stimulus-evoked change in light reflectance of the cortical tissue. The signal consists of three components whose relative contribution depends on the wavelength of the light (Frostig *et al.*, 1990). The first component is due to the difference between light absorption of deoxyhemoglobin and oxyhemoglobin. Oxygen consumption of activated neurons leads to an increase of deoxyhemoglobin. This oximetry component is largest around 610 nm. Another component, which dominates between 400 and 600 nm, originates from changes in blood volume. Dilatation of vessels or capillaries in active areas lead to greater absorption of light. The third component becomes significant at high wavelengths and is due to light scattering changes. The amplitudes of the optical signals are 0.01 - 0.1 % of the light reflected from the resting unstimulated brain surface. The signals are larger for lower wavelengths, but so are noise artifacts. Functional maps measured at different wavelengths are very similar. The spatial resolution obtained is high (~100  $\mu$ m), but due to the hemodynamic origin of the signal the temporal resolution is low (~1 s).

A standard recording method is used (e.g. Bonhoeffer and Grinvald, 1993). The cortex is illuminated by two fiber optic light guides. A video camera mounted above the cortex perpendicular to its surface grab images during and after stimulus presentation. The camera is focused 400 - 500 mm below the cortical surface. Two lenses with a large aperture ( $f/1.2$ ) are used to construct a macroscope whose shallow depth of field reduces artifacts due to vessels at the cortical surface. An analog amplifier enhances the video signal by subtracting a reference image (obtained when the animal views a blank screen) from the stimulus-evoked signals (obtained when the animal views one of a number of different stimulus patterns). After craniotomy, a stainless steel chamber (16 - 20 mm diameter) is cemented around the craniotomy, the dura removed and the chamber filled with silicone oil and sealed with a glass plate.

During the experiment, expired carbon dioxide and arterial oxygen saturation are monitored by a combined capnometer and pulse oximeter. Normal oxygenation of arterial haemoglobin is crucial for optical imaging. To this end, the animals are normally ventilated with oxygen (40 - 100% dependent on

anesthesia).

## Results

### *Areas 17 and 18*

These two areas can be activated separately by adjusting the visual stimuli presented to an experimental animal (see Figure). By varying the spatial frequency of drifting sinusoidal gratings we observed strong activation of area 18 at low spatial frequencies, but not at much higher spatial frequencies. Area 17 showed the opposite pattern of activation. These results show very clearly that area 17 is specialized for processing fine detail (high spatial frequencies) in a visual scene while area 18 shows selectivity for coarser details. The next stage of research will be to examine the effects of the temporal properties of a visual stimulus on activity in these brain regions.

### *Disparity processing*

Preliminary data have not revealed obvious aggregation of neurons selective for particular disparities. However, recent improvements in techniques may allow us to reveal some disparity-based organization in future work.

### *Marmoset visual cortex*

We have made good progress with work on marmoset cortex (Sengpiel et al 1996). We have so far concentrated on V1, in which we have had considerable experience in single-neuron recording. We have used horizontal and vertical drifting gratings, to demonstrate that the marmoset has an orientation columnar system that is qualitatively similar to that of the Old-world monkey. We plan to examine the detailed topography of the orientation columnar system, and to search for evidence of ocular dominance columns. Later we shall move on to extrastriate areas, to define areas and networks engaged by different sorts of visual stimuli.

## **Psychophysical studies of motion processing, binocular rivalry and ambiguous perception in human vision**

Recent observations showing similarities between binocular rivalry and other ambiguous percepts suggest that all viewing conditions entail competition for perception between different stimulus representations in the scene (Logothetis *et al.*, 1996; Andrews and Purves, 1997). If stimulus elements are similar they are grouped into a single representation, whereas if they are dissimilar they form multiple representations that can potentially compete for perceptual dominance.

A similar problem applies to moving images where the visual system must often decide whether motion signals arise from single or multiple objects. We suggest that the degree to which motion signals are perceived as being from the same object (or not) also depends on how they are grouped by the visual system according to their salient features. To test this hypothesis, we have compared the effects of changing various stimulus parameters (color, velocity, spatial frequency, orientation and contrast) in three ambiguous motion percepts - plaid motion, the barber pole illusion and binocular rivalry.

## **Methods**

As in our other vision experiments, stimuli were generated by a VSG graphics card linked to a high-frequency monitor. Testing was conducted in a darkened room. Ferro-electric shutter goggles that are compatible with the VSG card were used to generate binocularly rivalrous stimuli.

## Results

### 1. *Three illusions of motion perception*

A special case of an ambiguous motion stimulus arises when two independently moving orthogonal gratings are superimposed as a 'plaid' (see above: Adelson and Movshon, 1982; Stoner, Albright and Ramachandran, 1990). If the gratings are similar they tend to cohere and move unambiguously in a single direction (pattern motion). If, however, the two component gratings are of a different color, velocity, contrast or spatial frequency the component motion of each grating tends to predominate over the plaid motion. Another example of an ambiguous moving stimulus occurs when an obliquely oriented grating moving in a square aperture is perceived to alternate between horizontal and vertical motion (barber pole illusion). If several square apertures containing identical gratings are presented in different parts of the visual field, the alternation between horizontal and vertical motion is often concordant. Changing stimulus parameters such as color, velocity and spatial frequency in one aperture, however, reduces the concordance of the alternations. Similarly in binocular rivalry, as the images in the two eyes become increasingly different, the competition between the right and left eye views becomes more robust and the number of alternations increases. In conclusion, if moving objects share similar features (i.e. color, velocity, spatial frequency), they are grouped into a single stimulus representation, whereas, if they are dissimilar, they form multiple representations that can potentially compete for perception.

### 2. *Parallel processing of orientation and direction of motion*

Moving, sinusoidal gratings of different orientation, hue, or spatial frequency presented independently to the two eyes exhibit robust rivalry often resulting in complete perceptual dominance of one or the other grating. If the two eyes see achromatic gratings of similar contrast and velocity of motion, but differing substantially in orientation, the patterns usually break up into a patchy mosaic, with different regions of space being dominated by the individual gratings. Now, for some of the time, each individual patch appears to me moving orthogonal to the contours it contains (local component motion). However, the patches of differently oriented gratings are often perceived to move together in a direction that is the vector average of the two grating velocities (pattern motion). Thus the orientation of the two gratings continues to rival while the motion signals independently combine. This combination of motion signals is similar to when two orthogonal gratings are presented within a single aperture. These results show that direction of motion and orientation are processed independently and demonstrate that it is the representation of a stimulus, rather than a non-specific interaction between the monocular circuitry related to the two eyes, that competes in binocular rivalry (Andrew and Blakemore, 1999).

### 3. Very recently, we have been continuing our interest in perceptual ambiguity with neuroimaging techniques (functional Magnetic Resonance Imaging). We have asked how activity changes in the human cortex as perceptual interpretation changes for an ambiguous image. We chose to concentrate on the Rubin vase-face illusion, in which a vase shape on a contrasting background is alternately perceived as a vase or a pair of profile faces. We have shown that unambiguous images (photographs) of real faces specifically activate two regions of the occipital cortex, while inanimate objects activate a region in the parahippocampal gyrus. We then tracked the level of activation in these cortical voxels while subjects viewed a modified version of the Rubin illusion, in which perception switched from vase to face interpretations. Preliminary results suggest that there are differences in activity in the main face-sensitive area, depending on the nature of the perceptual interpretation.

## **Electrophysiological and psychophysical studies of human motion perception**

The AFOSR grants have partly supported work under two collaborations on electrophysiological indicators of motion processing in the human visual cortex. The first, with Drs Miroslav Kuba and Zuzana Kubová of the Medical Faculty of Charles University in Hradec Kralové, Czech Republic, and Dr Henk Spekreijse of the University of Amsterdam, involves the recording of evoked potentials (gross electrical responses recorded from the scalp). Kuba and Kubová (1992) described a specific signal, a negative component, with a peak latency of 150-250 msec (depending on stimulus contrast), produced by the onset of movement of a checkerboard pattern. This response is clearly distinguishable from the well-known positive going pattern-onset, pattern-offset and pattern-reversal responses, which almost certainly arise from the striate cortex. The motion signal is recorded optimally with an electrode placed some 5-10cm anterior to the occiput, over the presumed motion area in the human brain that has been revealed with neuroimaging (e.g. Mora et al. 1989; Corbetta et al. 1991; Zeki et al. 1991; Watson et al. 1993). The more posterior part of this area is thought to be homologous to the area MT or V5 in the monkey cortex, perhaps together with the equivalent of area MST (where cells responding to rotational and linear optic flow patterns have been described in the macaque monkey). But there is at least one additional motion sensitive area, more anterior in the human cortex, detected in recent neuroimaging studies, which may have no equivalent in the non-human primate.

The recording of evoked responses, previously somewhat out of favor, is experiencing a revival, partly because of advances in multi-electrode recording and dipole localization, but mainly because the results can be correlated with the results of single-neuron recording in monkeys and with neuroimaging studies in humans. Our plan has been to record visual evoked potentials (VEPs) for motion onset as a basis for studying the neural basis of motion processing in the human brain.

### **Contrast-dependence of VERs for pattern and motion**

Since MT in monkeys has its principal input from the high-contrast magnocellular (M) pathway, we set out to study the contrast-dependence of the motion-onset VEP, by comparison with the familiar  $P_{100}$  positivity (100 msec peak latency) produced by pattern reversal. We started by studying both types of VEP for checkerboard stimuli over a range of contrasts from 1.3% to 96% (Kubová et al. 1995).

The main findings were as follows:

- Whereas the amplitude of the  $P_{100}$  peak in both the pattern-reversal and the motion-onset VEP decreases in amplitude and increases in latency with reduction of contrast (to disappear at a contrast of about 2.3% for the motion-onset VEP at mid spatial frequencies), the amplitude of the later negative peak (produced best by the onset of motion) does not vary significantly with contrast, right down to 1.3%.
- The increase in peak latency of both types of VEP with reduction of contrast is much more pronounced for the positive components than for the negative ones.

Taking into account the characteristics of the magnocellular system (thought to be responsible for the detection of contrast at mid to low spatial frequencies and the processing of motion) and of the parvocellular system (probably responsible for processing of form and color), our findings strongly support the proposal that the  $N_{200}$  motion-onset signal arises from the extrastriate motion area with primary input from the magnocellular system, whereas the  $P_{100}$  component almost certainly arises from

the striate cortex.

Work in Amsterdam, in collaboration with the laboratory of Henk Spekreijse, has used a combination of multi-electrode recording and dipole analysis, together with SPECT imaging to provide further evidence for this interpretation.

### **Relation between electrical activity and the psychophysical detection of moving stimuli**

We followed up these results, making use of a new computer display system to generate stimuli of much lower contrast. We find that the amplitude of the specific motion-onset VEP does begin to decline at extremely low contrasts, approaching the psychophysical threshold for the detection of motion, whatever the spatial frequency of the pattern. Inspection of individual sweeps in response to near-threshold stimuli suggested that there may be a precise correlation between electrical and psychophysical responses, with undetected stimuli failing to elicit any signal and stimuli that **are** seen producing reliable, only slightly attenuated motion-onset VEPs.

### **Motion and pattern signals in amblyopic children**

In view of some psychophysical evidence that the analysis of motion is less severely affected than detection of pattern in developmental amblyopia, we studied VEPs in a large group of amblyopic children, with known aetiology (Kubová et al, 1995).

VEPs produced by pattern reversal were compared with those elicited by onset of motion in 30 amblyopic children (14 with anisometropic amblyopia, 6 with strabismic amblyopia and 10 with both anisometropia and strabismus). The amplitudes and peak latencies of the main  $P_{100}$  peak in the pattern-reversal VEP and of the motion-specific  $N_{200}$  peak in the motion-onset VEP through the amblyopic eye were compared with those through the normal fellow eye.

Regardless of the type of amblyopia, pattern-reversal VEPs through the amblyopic eye had significantly reduced amplitudes and prolonged latencies. In contrast, neither the amplitudes nor the latencies of the  $N_{200}$  motion-onset VEPs differed significantly between amblyopic and non-amblyopic eyes.

For pattern-reversal VEPs through the amblyopic eyes, the extent to which amplitude was reduced and latency increased correlated well with the reduction of visual acuity, whereas the amplitudes and latencies of motion-onset VEPs did not vary with visual acuity.

These results suggest that the source of motion-onset VEPs (probably an extrastriate motion sensitive area) is much less affected in amblyopia than that of pattern-reversal VEPs (probably the striate cortex). The motion pathway, presumably deriving from the magnocellular layers of the lateral geniculate nucleus (LGN), may be relatively spared in amblyopia.

### **A specific deficit of the motion system in developmental dyslexia**

A recent controversial hypothesis suggests that developmental dyslexia is commonly associated with a reduction in the number and size of cells in the magnocellular layers of the LGN, resulting in a range of psychophysical and oculomotor deficits. In view of the strong evidence (see above) that the motion-onset VEP arises from a part of the extrastriate cortex that is dominated by input from the magnocellular system, we examined motion-onset VEPs, as well as pattern-reversal VEPs, in 20

dyslexics and 17 controls (both with mean age of 10.0 years). Though we were initially doubtful of the 'magnocellular hypothesis', our results provided clear evidence for a specific and substantial defect in the motion pathway in the majority of dyslexic children.

Whereas the latencies and amplitudes of the main positive peak of pattern-reversal VEPs did not differ significantly between the dyslexic and control group, the motion specific negative peak of motion-onset VEPs was obviously **delayed** compared with normal in 27 out of 39 dyslexics ( $p < 0.001$ ), while there was no obvious reduction in its amplitude. This effect on the motion signal is very similar to the effect of reducing the contrast of the stimulus.

Our results support the notion of a selective magnocellular pathway disorder in many dyslexics and suggest that motion and pattern signals in the visual system may be temporally dissociated in the dyslexic brain. Motion-onset VEPs might provide an objective method for early diagnosis of this type of dyslexia.

### **Psychophysics and electrophysiology of second-order and 'cognitive' motion**

Through this collaboration we have been able to develop a laboratory for dense-array recording of human EEG in Oxford, and we continue to collaborate in the development of new computer graphics techniques. The computer systems that we have available in Hradec Kralov  and Oxford, controlled by versatile animation software, are enabling us to explore aspects of the perception of motion and to perform correlated tests of motion-onset VEPs to unusual, higher-order motion stimuli.

Of all the stimuli, moving random dots and exploding or imploding rectangular frames were most effective, the latter two being best for selective peripheral stimulation. Excellent motion VEPs are produced by onset of movement of pure chromatic stimuli (e.g. isoluminant red/green checkerboards or red dots on an isoluminant green background), implying input from the parvocellular system to the motion area (in agreement with recent work on the monkey). We are now testing a variety of second-order moving stimuli (not detectable by a pure linear Fourier analytical system), as well as various stimuli that appear to move but contain no explicit lateral displacement of correlated elements. All of these appear to elicit clear motion VEPs. We have also started to use the animation software to generate moving pictures that should be valuable in attracting the attention of young children during electrophysiological experiments.

### **Influences of attention on the processing of pattern and motion in the central and peripheral field**

I (Colin Blakemore) spent the 1995-96 academic year on sabbatical leave and was fortunate to be able to work at the University of California, Davis. Partly with the support of the AFOSR grant, I collaborated with the laboratory of Dr Ron Mangun, an expert in multi-electrode recording of event-related potentials, in correlation between such recordings and neuroimaging in humans, as well as in the mechanisms of attention. We studied the way in which voluntary, cued shifts of attention alter the responses to pattern reversal and motion onset stimuli in the central and peripheral visual field. In particular we examined whether selective attention to one aspect of a visual stimulus is correlated with selective enhancement of the corresponding component of the VEP and the corresponding cortical area identified by neuroimaging. It is already clear that both the (extrastriate) motion VEPs and the (presumed striate) pattern VEPs are augmented when the corresponding aspect of the visual stimulus is voluntarily attended. These studies are continuing.

# Residual motion processing ability ('blindsight') in the absence of human primary visual cortex

## Background

As part of our program of work to define the way in which information, especially about moving visual stimuli, is processed in different cortical areas, we have extensively examined the detection and discrimination of visual stimuli in a well-studied brain-damaged patient, GY. His left primary visual cortex (area V1), but not surrounding extrastriate areas, was virtually completely destroyed when he was 11 years old. Under particular conditions of stimulation we have been able to replicate findings of 'blindsight' behaviour – above-chance performance in detection and discrimination without conscious visual experience of the stimulus (see Weiskrantz, 1986). Our experiments have elaborated on the standard paradigms and are directed towards understanding the conditions necessary for obtaining detection without awareness.

Ablation of V1 removes direct cortico-cortical connections to motion processing centers (such as area MT) in the human and non-human primate brain. Weak residual input to MT and beyond is presumed to be due to subcortical projections from thalamic nuclei, especially the pulvinar, whose input derives from the superior colliculi (SC), but possibly also the lateral geniculate nuclei (LGN).

## Methods

While GY maintained fixation (monitored by infra-red detectors), we stimulated his blind right visual field. Scattered light emanating from the stimulus was rendered undetectable by flooding the intact left field with bright light. Responses were either verbal or involved interactive use of decision keys. Stimuli typically moved upwards, downwards, or rightwards (away from the spared central macular area).

## Results

High-contrast, high-velocity stimuli presented to the 'blind' field are quite apparent to patients such as GY. With low-contrast achromatic displays GY is able to detect and discriminate the direction of movement even at low velocity (over 5 – 10 deg/sec). As velocity increases so does the reliability of his performance as also his self-reported awareness, presumably reflecting increasing signal strength reaching spared motion center(s). At very low velocities (though still well within the range of perception in the normal visual field - 0.5 – 2.5 deg/sec), GY is apparently unable consciously to detect stimuli or to discriminate the direction of movement. At critical velocities, around 5 deg/sec, GY's discrimination performance can be well above chance level while he remains unaware of the visual event, i.e. blindsight. Similar psychometric observations prevail when contrast is the dependent variable at sub-threshold velocities. Experiments using isoluminant color-opponent stimuli (red and green, blue and yellow) indicate GY is also able to utilize such pure colour boundaries in detection and discrimination of moving stimuli (Guo *et al.*, 1998).

Our experiments have indicated that task loading and reporting instructions affect blindsight discrimination performance in GY (Benson *et al.*, 1997, 1998), in ways that resolve perplexing contradictions in the literature.

1. Discrimination performance improves if fewer psychophysical responses are required of him on each individual trial.
2. If required to report his degree of awareness **before** guessing the direction of motion of the stimulus, the frequency-of-seeing curves for the two reports are closely locked together.



3. If, on the other hand, the guess is requested first, discrimination performance improves considerably while the threshold for conscious perception stays remarkably fixed.
4. With the provision of performance feedback on each trial GY is able internally to adjust his response criterion – performance is improved while he remains unaware of stimulus displacement, thus blindsight behavior is more manifest.
5. Motion discrimination is improved further by single reports, yoked with feedback.

Together, our data suggest that blindsight behavior must be additionally characterized by the ability to associate weak motion signals of subcortical origin with directed report. Performance can be manipulated at the will of the experimenter: in particular, the subject's orienting instructions play a crucial role in establishing the criteria for motion signal characterization. The continued lack of access consciousness under these conditions is remarkable since the dissociation between accurate criterion-influenced 'guessed' report and absence of visual awareness persists.

We have continued to investigate the boundary conditions of GY's failed awareness for motion detection and discrimination. Stimulation has also been carried out using second-order motion stimuli. Despite the presumed absence or paucity of cortico-cortical projections that are thought normally to subserve analysis of pattern motion vectors in MT (see above), GY can quite reliably discriminate the (pattern) direction of motion of plaid stimuli. He is also able to detect the coherence of moving dot patterns when masked by a significant fraction of randomly moving dot elements, although his coherence threshold is much higher than normal (Benson et al., 1998). Current studies are aimed at characterizing 'neurometric' patterns of visual evoked potential fields (VEPs) recorded from GY's scalp in relation to his psychophysical performance. These preliminary experiments have yielded data that indicate stimulus-related VEPs over frontal brain structures (putatively, area 46) which suggest activation around (at least) this area may be directly correlated with the mode of conscious experience and behavioral report.

### **Neuroimaging studies of the processing of visual motion and optic flow, and the integration of visual and vestibular information in the human brain**

An important part of the proposal for the AFOSR grant was to study the brain mechanisms for the interpretation of optic flow, i.e. the global patterns of retinal movement that result from self-motion of an observer in space. As a person moves through space (for instance, when flying an aircraft) his or her own motion creates correlated flow of the image or one or more of the following types:

- Radial flow (expansion when moving directly forward; contraction when reversing);
- Roll (circular movement around the center of heading, created by rotation of the head around a sagittal axis); and
- Yaw or Tilt (translational movement of the image caused by rotation of the head around an axis in the coronal plane).

The AFOSR grant supported an extensive collaboration with Drs Previc and Beer of Brooks Air Force Base and Liotti and Fox of the University of Texas Research Imaging Center in San Antonio. We used a special optical system designed by Dr Previc, incorporating a very large screen and a collimating Fresnel lens (creating a field subtending more than 100° in width). Through this system, volunteers viewed sophisticated, computer-generated patterns created in real-time, while local cerebral blood flow was monitored by Positron Emission Tomography (PET).

The stimuli included accurate simulations of the retinal motion associated with fore- or aft- movement,

horizontal yaw and roll. These patterns, when presented over wide areas of the visual field, produced compelling sensations of self-motion ('vection'). The activations produced by such flow patterns were compared with those produced by precisely matched control stimuli in which the size and velocity characteristics of the tiling elements were well matched to those of the corresponding flow pattern, but the directions of motion were randomized for each tile, and with those produced by static arrays of tiles, matched in size and density to those in the moving displays.

The results of these studies have provided valuable new information into the way in which optic flow information is processed in the human brain and the probable mechanisms of integration of these signals with those from the vestibular system. This area of research is particularly relevant to flying skills, to the illusions resulting from discordant visual and vestibular stimulation, and to spatial disorientation in flight.

We employ several different stimulus conditions for each subject, including flow stimulation of the entire display (which generates a strong sense of **vection** or self-movement) and similar stimulation of only the central 50 deg of the field, which does not. We also take scans with the subject viewing a static array of dots and an array of moving dots identical to that in the flow stimulus except that their trajectories are randomized rather than ordered to generate a flow pattern.

## Results

- 1) A global analysis across the three types of flow stimuli identified brain areas that respond to the displays' shared characteristic of coherent, wide-field motion, versus incoherent motion. Such areas were identified in the posterior-inferior temporal cortex (Brodmann Area 37), paralimbic cortex, pulvinar, and midbrain tegmentum.
- 2) Full-field flow patterns did **not** significantly activate the so-called 'motion area' in the lateral occipital cortex, thought to be equivalent to the areas MT and MSTd in monkeys, where neurons respond to linear motion and flow patterns respectively. This unexpected result challenges the generally accepted homology of function with the monkey areas.
- 3) Wide fields of sparse, randomly moving elements **do** activate the classical human 'motion areas'.
- 4) The 'kinetic motion area' (KO), adjacent to V3 and previously thought to be specifically responsive to kinetic boundaries (neighboring regions of differently moving texture), responds well to flow stimuli with significant differences in nearby vectors of motion (radial flow and roll, but not yaw).
- 5) The presumed connectivity of the network of major sites responding specifically to coherent motion was analyzed using *regional regression*.
- 6) A large network of unexpected areas, normally associated with the vestibular system, are also activated by wide-field flow stimuli, including the primary vestibular nuclei, parts of the cerebellum, the right insula and the putamen. The coherent motion mechanisms included subcortical and limbic structures, known to receive polysensory input and thought to be implicated in postural regulation, navigation, and arousal.
- 7) Both roll and yaw stimulation reliably activate a vast, distributed array of lateralized cortical and cerebellar areas, with hemispheric asymmetry corresponding to the direction of roll or yaw motion.

These results have been published in part (Previc et al, 2000, 2001), but further publications are in preparation.

## Conclusion

Virtually all of the objectives proposed in the original applications for support from the AFOSR have been accomplished. A very wide range of multidisciplinary research has been completed, leading to a large number of publications and to a substantial increase in our understanding of the way in which retinal motion information is processed in the brain. The grant has enabled us to move rapidly into important new areas of research, using facilities (such as the dense-array scalp recording system and the optical imaging equipment) provided by the Medical Research Council.

We are immensely grateful to the AFOSR for this valuable grant and we hope that our productivity and the breadth and novelty of our work will be judged to have justified the support.

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